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Laboratory Experiments on Mechanisms of Competition and Resource Partitioning between 'Menidia menidia' (L.) and 'Menidia beryllina' (Cope) (Osteichthyes:Atherinidae)

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16. ABSTRACT

Postlarvae of two atherinid species, Menidia menidia (L.) and Menidia beryllina (Cope), were tested in two 14-day experiments at four densities of fish to determine effects of interspecific versus intraspecific competition for food. In one experiment, when M. menidia was slightly larger than M. beryllina (simulating a slightly earlier hatching time in nature) M. menidia exhibited a clear competitive advantage over M. beryllina, as demonstrated by covariance analysis of fish biomass change on fish density. In the second experiment, when M. beryllina was larger than M. menidia, neither species showed competitive advantage. The results suggest that M. menidia has an inherently superior ability to compete for food. Results of the experiment in which M. menidia was the larger species indicate the selective pressures which could have caused the two species to evolve spawning times ca. 1 month apart.

In another set of experiments, post-larval and juvenile M. menidia and M. beryllina were fed varying rations of Artemia nauplii during a series of three 10-day feeding trials. As Menidia menidia grew, they required a smaller percentage of body weight per day in food for maximum growth. The same trend was observed with M. beryllina, although the percentages were much less than those for M. menidia. Menidia menidia also required more food per day as a minimum ration for survival and growth than did M. beryllina. The explanation for these differences may be that M. menidia in nature hatch earlier in the year, when zooplankton is more abundant, than do M. beryllina. The two species have apparently evolved different feeding requirements as adaptations to the different food availabilities that they encounter.

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LABORATORY EXPERIMENTS ON MECHANISMS OF COMPETITION AND RESOURCE PARTITIONING BETWEEN *MENIDIA MENIDIA* (L.) AND *MENIDIA BERYLLINA* (Cope) (OSTEICHTHYES:ATHERINIDAE)[1]

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Abstract: Postlarvae of two atherinid species, *Menidia menidia* (L.) and *Menidia beryllina* (Cope), were tested in two 14-day experiments at four densities of fish to determine effects of interspecific versus intraspecific competition for food. In one experiment, when *M. menidia* was slightly larger than *M. beryllina* (simulating a slightly earlier hatching time in nature) *M. menidia* exhibited a clear competitive advantage over *M. beryllina*, as demonstrated by covariance analysis of fish biomass change on fish density. In the second experiment, when *M. beryllina* was larger than *M. menidia*, neither species showed competitive advantage. The results suggest that *M. menidia* has an inherently superior ability to compete for food. Results of the experiment in which *M. menidia* was the larger species indicate the selective pressures which could have caused the two species to evolve spawning times ≈ 1 month apart.

In another set of experiments, post-larval and juvenile *M. menidia* and *M. beryllina* were fed wet weight rations of *Artemia* nauplii ranging from 10–640% of initial body weight per day during a series of three 10-day feeding trials. As *Menidia menidia* grew, they required a smaller percentage of body weight per day in food for maximum growth (640, 320, and 160% for the three feeding trials). The same trend was observed with *M. beryllina*, although the percentages (160, 160, and 80%) were much less than those for *M. menidia*. *Menidia menidia* also required more food per day (20–135% of body weight) as a minimum ration for survival and growth than did *M. beryllina* (5–60%). The explanation for these differences may be that *M. menidia* in nature hatch earlier in the year, when zooplankton is more abundant, than do *M. beryllina*. The two species have apparently evolved different feeding requirements as adaptations to the different food availabilities that they encounter.

Key words: fish competition; *Menidia menidia*; *Menidia beryllina*; resource partitioning; fish growth

INTRODUCTION

Competition between fish species in nature is often hypothesized on the basis of similar food and/or habitat requirements. In relatively few instances, however, has competition between fishes been demonstrated experimentally. Occasionally, "natural experiments" comparing allopatric and sympatric populations of two species have

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shown interactive segregation likely to be due to competition in the area of sympatry (Nilsson, 1965; Andrusak & Northcote, 1971). Werner & Hall (1976, 1977, 1979) employed an outdoor laboratory arrangement of 18 identical ponds to demonstrate the effects of competition among three centrachid species. Using aquaria, Laurence *et al.* (1981) investigated competition for food by larval cod (*Gadus morrhua*) and haddock (*Melanogrammus aeglefinus*) at several prey densities. Haddock larvae did not grow as well as cod, but the results were not conclusive because the cod larvae may have preyed upon the haddock. McComas & Drenner (1982) found that juvenile *Menidia beryllina* could outcompete juvenile *Labidesthes sicculus* in laboratory aquaria because *Menidia beryllina* was better able to capture copepod prey.

Fish biologists have not utilized the experimental design and covariance analysis for competition that Fraser (1976) employed in his studies of salamander competition. Fraser's method, which utilizes a fixed prey density and varying predator density, served as a model for the competition studies with the Atlantic silverside, *M. menidia* (L.), and inland silverside, *M. beryllina* (Cope), described herein.

Atlantic and inland silversides are sympatric along the eastern coast of North America with *M. menidia* ranging from the Gulf of St. Lawrence, Canada, to Florida, U.S.A., and *M. beryllina* from Cape Cod, U.S.A., to Mexico (Johnson, 1975). Both species spawn after 1 yr and have life cycles of <2 yr. They feed, particularly during the younger stages, primarily on small planktonic crustaceans and are important as forage fish for larger fish species in the estuary (Bigelow & Schroeder, 1953). They are important laboratory subjects for toxicity tests (Anderson *et al.*, 1974; Middaugh & Dean, 1977; Voyer et al., 1979; Hollister *et al.*, 1980), and are cultured in the laboratory for that purpose (Beck, 1979).

In Rhode Island estuaries, these two atherinid species overlap substantially in habitat within the estuary and eat similar foods (Bengtson, 1982, 1984). However, *M. menidia* spawns ≈ 1 month earlier in the upper estuary and grows more rapidly than *M. beryllina*, so that *M. menidia* young of the year (YOY) are almost always larger than *M. beryllina* YOY (Bengtson, 1984). Quite possibly, larger size might confer a competitive advantage on *M. menidia* YOY in the field.

In the first part of the study reported here, competition for food was examined under laboratory conditions in two experiments to test the hypotheses that (a) competitive advantage is gained on the basis of body size alone, or (b) competitive ability is greater in one of the species, regardless of body size. In Experiment I, *M. menidia* individuals were slightly larger than *M. beryllina*, although the difference was not nearly as large as that observed in nature. Thus, the results indicate what would happen in nature if *M. menidia* spawned only slightly earlier than *M. beryllina*. In Experiment II, *M. beryllina* individuals were larger than *M. menidia*, a situation which has not been observed in nature. If the initially larger species "won" the competition (i.e., grew proportionately more) in each experiment, hypothesis (a) would be supported; if not, hypothesis (b) would prevail. The required differences in body size were obtained by controlling spawning and growth in the laboratory.

In the second part of this study, effect of food ration size on growth and survival of laboratory populations of *M. menidia* and *M. beryllina* was investigated. The two reasons for this second series of experiments were (a) that it is useful for purposes of laboratory culture to know these species' optimal food ration sizes, and (b) as part of my studies on resource partitioning by *M. menidia* and *M. beryllina*, it became necessary to determine, given the fish and prey abundances observed in the estuary, whether food was a limiting resource there. Bryant & Matty (1980) found that, for optimal growth, carp (*Cyprinus carpio*) larvae required 200–250% of their body weight per day in *Artemia* nauplii during the first 5 days of feeding and 100–120% during the second 5 days. The general problem of sufficient food concentration or ration size has been reviewed by Kinne (1977) and Brett (1979).

Materials and Methods

CULTURE OF FISH

Fish used in the experiments were obtained from artificial spawnings of adult *Menidia menidia* and *M. beryllina* collected by beach seine in southern Rhode Island estuaries. Hand-stripping of eggs onto nylon screens, fertilization and incubation were according to the methods of Barkman & Beck (1976) and Beck (1979). After hatching, *M. menidia* larvae were fed ad libitum on newly hatched *Artemia franciscana* nauplii (Macau, Brazil strain) and *M. beryllina* larvae received ad libitum rotifers (*Brachionus plicatilis*) for 4 days (because their mouths were not large enough to ingest *Artemia franciscana* nauplii), then newly-hatched *A. franciscana* nauplii. In order to achieve the desired sizes of fish for the competition experiments, the *Menidia menidia* used in competition Experiment I were reared for 22 days, at temperatures of 18 ± 1 °C and salinities of 30 ± 1‰, while *M. beryllina* were reared for 9 days at 23 ± 1 °C and 30 ± 1‰. Competition Experiment II *M. menidia* were reared for 15 days at 21 ± 1 °C and 31 ± 1‰, while Experiment II *M. beryllina* were reared for 30 days at 21 ± 1 °C and 31 ± 1‰. Temperatures and salinities for egg incubation were the same as those for rearing.

COMPETITION EXPERIMENTS

Fish used in the competition experiments were removed from the stock tanks and placed in filtered sea water in the experimental chambers (37-l glass aquaria) at densities of 16, 32, 64, or 128 fish per aquarium (Fig. 1). One-third of the aquaria contained *M. menidia* only, one-third contained *M. beryllina* only, and one-third contained equal numbers of both species. Each density in each condition was tested in duplicate and the aquaria were placed in random order.

At the start of each experiment, 25 fish of each species were also taken from the stock tanks for determination of average total lengths and wet weights. Initial mean lengths and weights per fish were: Experiment I: *M. menidia* – 10.73 mm, 3.24 mg, *M. beryllina*

– 7.83 mm, 1.09 mg; Experiment II: *M. menidia* – 8.18 mm, 1.49 mg, *M. beryllina* – 13.91 mm, 12.20 mg. All fish were in the postlarval stage at the beginning of the experiments and some transformed into juveniles during the experiments.

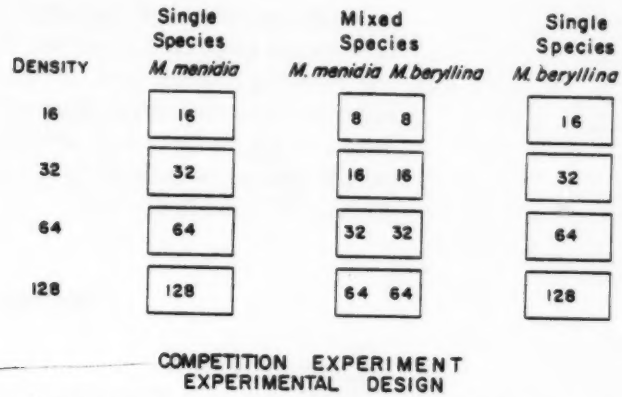

Fig. 1. Experimental design for both competition experiments described in the text: each rectangle represents a 37-l aquarium containing the number(s) of each species indicated within the rectangle.

The same amount of food was added to each aquarium each day, i.e., 100% of the initial wet weight of 45 members of the larger species in the experiment in wet weight of newly-hatched *Artemia franciscana* nauplii (mean length = 0.433 mm). From previous experiments (Bengtson *et al.*, 1978) an *Artemia* food ration of 100% of initial body weight was known to allow good survival and growth of *Menidia menidia* juveniles. The number 45 represents the midpoint in the exponential progression of densities used (i.e., $2^{5.5}$). Thus, fish at the lower densities received sufficient food for survival and growth, but fish at higher densities received insufficient food levels. Fish received the entire ration each day in a single feeding. The size of the food particles was similar to that of copepod naupliar and copepodite stages that postlarval *Menidia* would be eating in nature.

One-third of the water volume of each aquarium was changed each day by siphoning and refilling with filtered sea water immediately prior to feeding. Any dead fish were removed, counted and identified to species. I attempted to siphon all detrital and fecal material from the bottom of each tank daily, but not to remove all the live *Artemia* still present from the previous day's feeding. Because the *Artemia* had no food, they died within 1–2 days if not eaten by the fish. Light was provided to each aquarium at ≈400 lux by a 15 W Sylvania F15T8-EN Enhance* fluorescent lamp in the cover of each aquarium. Water in each aquarium was lightly aerated. Experiment I was conducted at 24 ± 2 °C and 31 ± 1‰, Experiment II at 23 ± 2 °C and 32 ± 1‰. Although the

* Mention of trade names does not constitute endorsement by the U.S. E.P.A.

average rearing temperatures were different from the average experimental temperature, the differences were typical of those that the species might experience over a daily cycle in nature. A thermal acclimation period of one day was therefore considered sufficient, especially since the maximum Δt during the 1-day acclimation was 3 °C.

At the end of each experiment (14 days), all surviving fish were removed and their total lengths and wet weights were recorded. From the weight data, change in biomass was calculated for each species in each aquarium according to the formula $W = (\ln B_t - \ln B_0)/t$, where B_t = final biomass, B_0 = initial biomass, and t = time in days. Finally, for each species in each condition (single or mixed species), W was plotted as a function of ln density. The slopes of the regression lines for each species in single versus mixed conditions were compared by analysis of covariance. Differences in slope were considered significant at the $P < 0.05$ level.

FOOD RATION EXPERIMENTS

Duplicate chambers for each of six ration size treatments plus one unfed control chamber were arrayed in random order on a laboratory bench. The six ration sizes of *Artemia* nauplii used were 20, 40, 80, 160, 320, and 640% of initial body weight per day on a wet weight food/wet weight fish basis. An experiment consisted of fish from one or the other species grown on the six feeding levels for a period of 10 days. Each species was tested in three separate experiments using individuals from different groups of parents for each experiment. The only exception to the ration size regime occurred in the last *Menidia beryllina* experiment when the 320 and 640% treatments were omitted and a 10% treatment was inserted in their place. Lack of growth of fish in the unfed control chamber in each experiment verified that insufficient food was introduced with the incoming filtered water to support growth and survival.

Because young silversides are planktivores, the experimental chambers provided a large ratio of water-column volume to bottom surface area. The chambers were cylindrical hatching jars (45.7 cm high, 15.2 cm in diameter) modified after those of Buss (1959) and were previously used successfully and described more fully in the silverside nutrition studies of Bengtson *et al.* (1978) and Beck *et al.* (1980). The experiment was run under semi-static conditions, with one-third of the 5.5-l volume of filtered sea water in each jar being changed each day.

At the start of each feeding trial, 25 fish of the species being tested were taken from a stock tank and placed into each hatching jar. A sample of 20 fish was also taken from the stock tank for initial measurements of total length and wet weight. Mean wet weight of a fish was then calculated and multiplied by 25 to obtain an estimate of the initial biomass of fish in each hatching jar. All hatching jars were assumed to have equal biomasses of fish at the start of a run, because young silversides are extremely delicate and individual fish could not be weighed and then used in an experiment. The food ration fed to each jar was calculated as the appropriate percentage of initial biomass.

Artemia franciscana cysts (Macau, Brazil strain) were hatched in filtered sea water in separatory funnels and stage I nauplii were harvested. After being collected on a 140-μm mesh screen, nauplii were blotted dry on a paper towel before rations were weighed out. Daily ration for each jar was placed in the jar immediately after weighing so that the nauplii would remain alive and freely swimming in the water column during the ensuing 24-h period.

Prior to feeding each day, one-third of the water volume in each jar was changed, the bottom was siphoned clean, presence of any remaining live food was noted, and any dead fish were counted and removed. No attempt was made to remove all the food remaining from the previous day because (a) it would have been impossible to do so without killing some fish in the process, and (b) nauplii died from lack of food after 1–2 days and were eventually siphoned away. On the first day after transfer of fish to the hatching jars, any dead fish observed were replaced, because these mortalities were assumed to be due to handling. After that, no mortalities were replaced. Rather, food amount to any jar was reduced proportionately as mortalities were observed in that jar.

At termination of each run, all fish in each jar were removed and total length and wet weight of each fish was measured. Total biomass of fish in each jar was then calculated. Percent change in biomass for each jar was obtained by subtracting initial biomass from final, dividing that by initial biomass and multiplying the result by 100. A linear regression was calculated for each experiment showing percent change in biomass as a function of ration size up to, but not including, the point at which percent change in biomass was not significantly larger (t-test; $P < 0.05$) than the percent change in biomass at the next lowest ration size tested. In one situation that was clearly non-linear, a quadratic function provided the best fit to the data.

Results

Competition experiments

When *Menidia menidia* was the larger species, it exhibited a competitive advantage over *M. beryllina*. In Experiment I, the regression line for *M. menidia* in the single species condition had significantly greater negative slope than that for *M. menidia* in the mixed condition (Fig. 2; Table I), while the regression for *M. beryllina* had a significantly less negative slope in single species condition than in mixed (Fig. 3; Table I). Thus, for *M. menidia*, intraspecific competition was greater than interspecific, whereas for *M. beryllina* the opposite was true.

In Experiment II, regression lines for both *M. menidia* and *M. beryllina* in single species conditions had relatively small slopes (Figs. 4 and 5; Table I). Results for both species in mixed condition produced functions that were not monotonically decreasing. Therefore, no comparison of slopes for species in single versus mixed conditions was possible. At the highest density of 128 fish per aquarium where the greatest competition presumably occurred, however, each species did as well in mixed species as in single

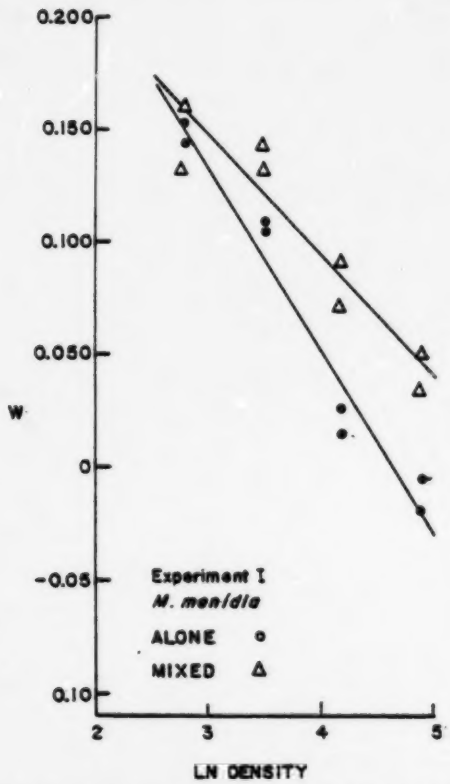

Fig. 2. Regressions of change in biomass on density for *Menidia menidia* in single and mixed species conditions in competition Experiment I: $W = (\ln B_t - \ln B_0)/t$, where B_t = final biomass, B_0 = initial biomass, and t = time in days.

TABLE I

Linear regression equations for two laboratory experiments on competition between *Menidia menidia* and *M. beryllina* of differing sizes: in Experiment I, *M. menidia* was the larger species, whereas *M. beryllina* was the larger in Experiment II; see Figs. 2–5 for graphical presentation of data points; in all cases, $W = (\ln B_t - \ln B_0)/t$, where B_t = final biomass in an aquarium, B_0 = initial biomass in an aquarium, t = time in days, and D = ln density, where density is density of fish in an aquarium.

Experiment	Condition	Equation	r value	ANCOVA results
I	*M. menidia* single	$W = -0.081D + 0.374$	0.96	$F = 7.75$; $P < 0.02$
	M. menidia mixed	$W = -0.053D + 0.306$	0.89	
	M. beryllina single	$W = -0.049D + 0.347$	0.84	$F = 9.16$; $P < 0.02$
	M. beryllina mixed	$W = -0.103D + 0.480$	0.88	
II	*M. menidia* single	$W = -0.022D + 0.262$	0.59	–
	M. menidia mixed	(no regression)	–	
	M. beryllina single	$W = -0.030D + 0.149$	0.81	–
	M. beryllina mixed	(no regression)	–	

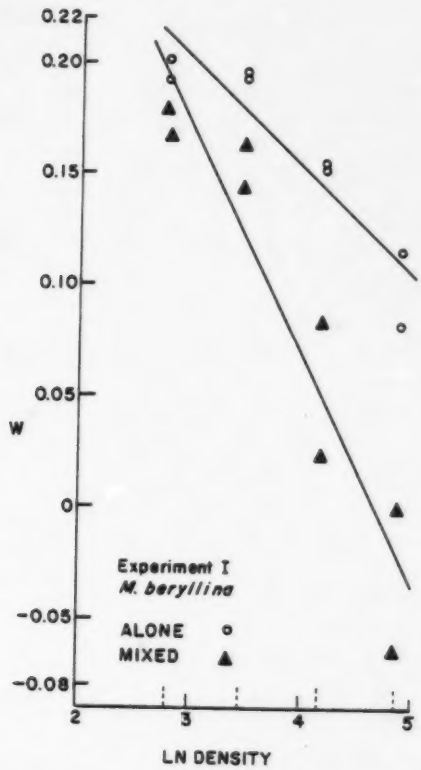

Fig. 3. Regressions of change in biomass on density for *Menidia beryllina* in single and mixed species conditions in competition Experiment I: $W = (\ln B_t - \ln B_0)/t$, where B_t = final biomass, B_0 = initial biomass, and t = time in days.

TABLE II

Regression equations for percent change in biomass of *Menidia menidia* and *M. beryllina* as a function of food ration size: Y = percent change in total biomass of fish in a hatching jar, X = food ration size in percent of wet fish body weight in wet weight of food per day.

Species	Initial wet wt/fish (mg)	Initial wet wt per hatching jar (mg)	Equation	r value
M. menidia	1.49	37	$Y = 1.46X - 47.65$	0.98
	13.36	334	$Y = 0.70X - 88.82$	0.93
	50.40	1259	$Y = 1.070X - 29.02$	0.78
M. beryllina	7.52	188	$Y = 1.30X - 10.73$	0.93
	12.20	305	$Y = 1.39X - 78.74$	0.99
	77.56	1939	$Y = 1.26X - 26.77$	0.87

species conditions. There was no significant difference (t-test; $P < 0.05$) in log-transformed biomass change between mixed and single species treatment for either *M. menidia* or *M. beryllina* at the highest density. Thus, when *M. beryllina* was the larger species, it did not outcompete *M. menidia*.

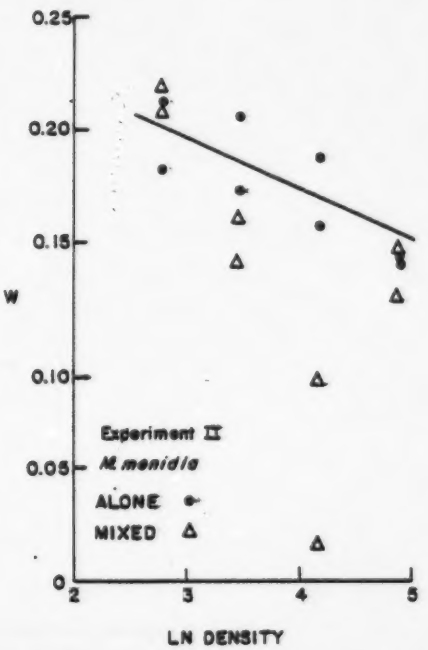

Fig. 4. Regression of change in biomass on density for *Menidia menidia* in single species condition in competition Experiment II: non-linear scattering of points representing biomass change with density for *M. menidia* in mixed species condition is also presented; $W = (\ln B_t - \ln B_0)/t$, where B_t = final biomass, B_0 = initial biomass, and t = time in days.

FOOD RATION EXPERIMENTS

The smallest *M. menidia* tested (initial mean wet weight of 1.49 mg/fish or 37 mg per hatching jar) totally consumed 320% of their body weight per day and nearly consumed 640% per day. These fish grew significantly more (t-test; $P < 0.05$) on 640% than on 320% (Fig. 6). Since only a few nauplii remained in the 640% treatment each day, one can assume that this group of fish was capable of clearing ≈500–600% of their body weight per day from the water. In the second run, fish that were larger (13.36 mg/fish or 334 mg per hatching jar) cleared only 160% of their body weight per day. The regression line for this group (Fig. 6) showed a plateau of growth at 320%. *M. menidia* of this size can consume, therefore, ≈250–300% of their body weight per day. The largest *M. menidia* tested (50.40 mg/fish or 1259 mg per hatching jar) were unable to

remove 160% of their body weight per day but could clear 80%. The growth plateau for this group (Fig. 6) appeared at 160%, so I estimate the feeding capability to be 100–150% of their body weight per day.

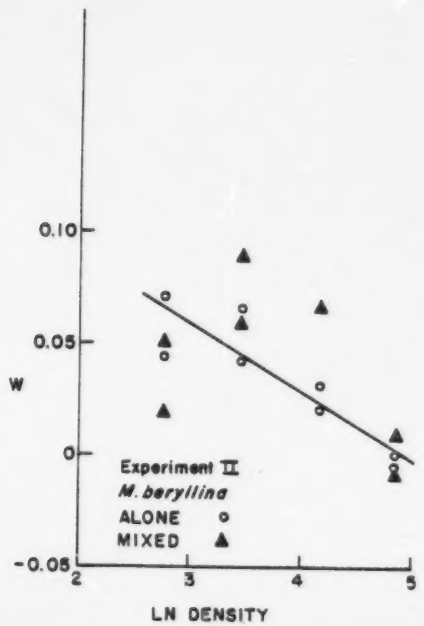

Fig. 5. Regression of change in biomass on density for *Menidia beryllina* in single species condition in competition Experiment II: non-linear scattering of points representing biomass change with density for *M. beryllina* in mixed species condition is also presented; the single black triangle at density = 64 actually represents two coinciding data points; $W = (\ln B_t - \ln B_0)/t$, where B_t = final biomass, B_0 = initial biomass, and t = time in days.

In contrast, the maximum amount ever cleared by *M. beryllina* was 160% of body weight per day and that was not done consistently. Usually, *M. beryllina* of initial mean wet weights 7.52 or 12.20 mg/fish (188 or 305 mg per hatching jar) totally consumed only 80% of their weight per day. The regression lines for those two groups (Fig. 7) nevertheless showed a growth plateau at 160%, leading to an estimate of daily food consumption of 100–150% of body weight per day. The largest *M. beryllina* tested (77.56 mg/fish or 1939 mg per hatching jar) ingested 80% of body weight per day, but never 160%, and the growth plateau for the group was at 80% (Fig. 7). The estimate of food consumption ability for this group, therefore, is between 80% and 100% of body weight per day.

The minimum ration required by fish of both species in order for growth to occur in population biomass can be estimated by noting the point at which each regression line

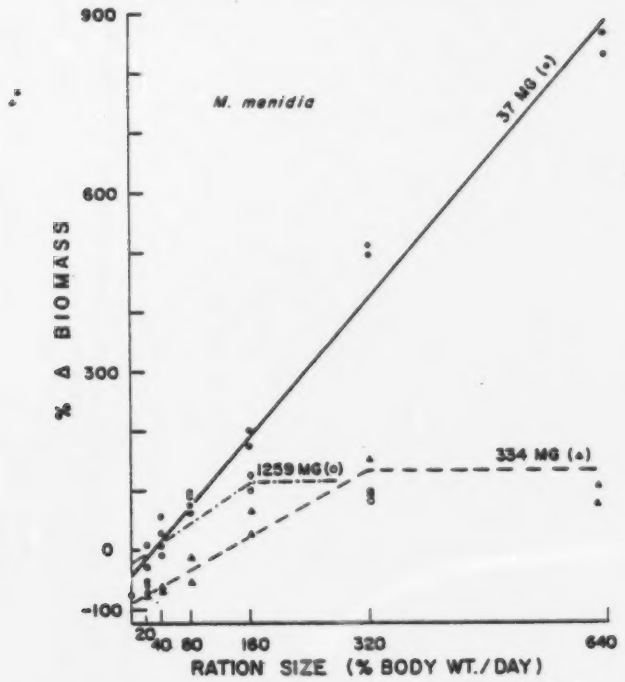

Fig. 6. Percent change in biomass as a function of food ration size for young *Menidia menidia*: ration sizes are given as percent of fish wet weight in wet weight of food per day; weight shown above each line indicates initial biomass per hatching jar (25 fish per jar) for that 10-day feeding trial.

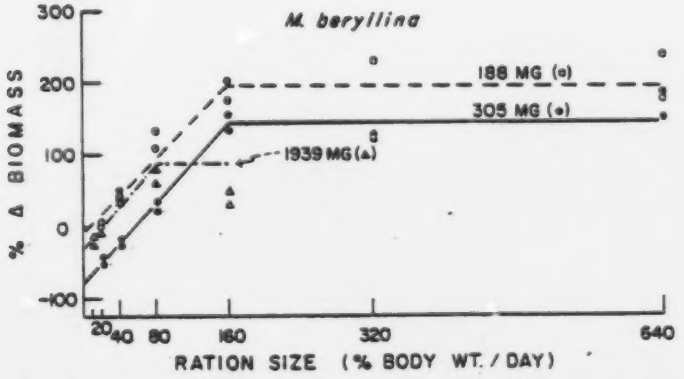

Fig. 7. Percent change in biomass as a function of food ration size for young *Menidia beryllina*: ration sizes are given as percent of fish wet weight in wet weight of food per day; weight shown above each line indicates initial biomass per hatching jar (25 fish per jar) for that 10-day feeding trial.

TABLE III

Number of mortalities observed in each replicate of experimental runs for *Menidia* spp. fed different ration amounts (% body wt/day): each run began with 25 fish per replicate; A and B are individual replicates within a treatment.

Species	Initial fish size (mg)	Ration amount														
		0	10		20		40		80		160		320		640	
			A	B	A	B	A	B	A	B	A	B	A	B	A	B
M. menidia	1.49	22	–	–	16	13	6	4	3	2	6	11	3	1	2	0
	13.38	24	–	–	16	20	19	19	12	17	11	13	7	8	8	9
	50.37	22	–	–	0	0	0	0	0	0	2	0	3	2	0	0
M. beryllina	7.51	10	–	–	0	1	0	0	1	0	1	1	0	0	1	0
	12.10	25	–	–	12	6	8	5	2	5	2	3	3	3	3	2
	77.56	14	0	3	2	0	2	2	0	0	1	1	–	–	–	–

intersects the line representing % biomass = 0 in Figs. 6 and 7. For the various sizes of *M. menidia* tested, ration required for zero biomass change varied from 20% to ≈ 135% of body weight per day. *M. beryllina* tested required only 5 to 60% of their body weight per day in order to maintain the biomass with which the experiment was begun. Loss of biomass was due primarily to mortalities (Table III) in a treatment rather than weight loss by survivors.

The data on mean individual weights, along with instantaneous rate of growth for individuals, are provided in Table IV. The data may not be as useful as similar kinds of data often collected for juvenile salmonids (see literature review by Brett, 1979),

TABLE IV

Mean absolute growth in weight and daily specific growth rates (%/day) of individuals in each food ration treatment: for each species, results are given for each of three feeding trials; for each replicate, upper number is mean growth in mg, lower number is growth rate.

		M. menidia			*M. beryllina*		
Ration	Replicate	1	2	3	1	2	3
10	A	–	–	–	–	–	−10.81
		–	–	–	–	–	−1.5
	B	–	–	–	–	–	−11.69
		–	–	–	–	–	−1.6
20	A	1.44	−2.86	−0.29	−1.86	−0.36	−4.08
		6.7	−0.6	−0.2	−1.7	−0.5	−0.5
	B	0.92	−7.57	0.65	−3.83	0.35	0.02
		4.8	−1.6	0.5	−3.8	−0.5	0.0
40	A	0.83	20.15	−0.64	0.35	4.24	41.12
		4.4	3.4	−0.5	0.3	4.5	4.3
	B	1.04	14.24	10.48	0.48	3.49	39.89
		5.3	2.5	5.8	0.4	3.8	4.1
80	A	2.17	48.07	10.95	5.97	9.23	43.75
		9.0	6.7	6.0	4.0	8.0	4.5
	B	1.76	45.40	4.64	6.78	9.69	59.06
		7.8	6.4	3.0	4.4	8.3	5.7
160	A	6.39	62.90	22.02	20.27	15.90	21.75
		16.7	8.1	9.7	9.8	15.6	2.5
	B	6.49	64.65	32.97	18.95	15.69	32.67
		16.8	8.3	12.4	9.4	11.3	3.5
320	A	11.90	60.30	27.08	16.63	16.85	–
		22.0	7.9	11.0	8.6	11.8	–
	B	7.40	47.85	31.00	20.33	17.39	–
		17.9	6.7	12.0	9.8	12.0	–
640	A	14.91	–	21.38	26.20	13.58	–
		24.0	–	9.5	11.5	10.3	–
	B	14.99	–	34.53	18.86	18.08	–
		24.0	–	12.8	9.3	12.3	–

because so many of the individual fish in the experiments died (particularly in low-ration treatments), and individual weights represent only the surviving fish.

In summary, it appears that *M. menidia* individuals are capable of consuming much more food per day than are *M. beryllina*, but the former also require more food per day to remain alive than do the latter.

Discussion

The conclusion to be drawn from the competition experiments considered together is that competitive ability is not a function of size differences at the beginning of the experiment, but that *M. menidia* probably is an inherently superior competitor. This conclusion is strongly supported by the superior performance of *M. menidia* when it was the larger of the two species in Experiment I and by its ability to survive and grow well at the highest density in competition with the larger *M. beryllina* in Experiment II.

No aggressive or territorial behavior was observed. Silversides are actively swimming, highly mobile, schooling fish which are more likely to engage in exploitative competition than in interference competition. The food ration experiments indicated that the maximum food intake of *M. menidia* juveniles is about double that of similarly sized *M. beryllina* on a daily basis.

Competition Experiment I was particularly instructive because it suggested the selective pressures that could cause the evolution of a separation of spawning times. Fish used in Experiment I differed by ≈ 4 mm in total length, a situation which in nature would mean that they had hatched about one week apart. The mixed species data in Fig. 2 show that not only does *M. beryllina* exhibit reduced growth in competition with *M. menidia* but that, at the highest density, the former is competitively excluded by the latter (ordinate axis value less than zero). In nature, periods of high fish density or low food availability immediately after fish hatching would lead to selection for individuals of the two species which hatched at more divergent times. Thus, the earlier-spawning *M. menidia* could grow to a size capable of ingesting larger food types before the later-hatching *M. beryllina* began consuming the smaller food types used earlier in the season by *M. menidia*. *M. menidia* spawns ≈ 1 month prior to *M. beryllina* in the upper portions of Rhode Island estuaries (Bengtson, 1982).

The poor performance of mixed-condition *M. menidia* at the medium densities in Experiment II is not easily explained. One outlying point in the density = 64 treatment suggests that there may have been a problem peculiar to fish in that one aquarium (e.g., disease or leaching of a toxic chemical), but no particular anomalies were observed.

The initial fish sizes that were used in the competition experiments were chosen so that two hypotheses could be tested in the limited amount of time that the experimental facilities were available. Had it been possible it would have been desirable to conduct two more experiments, (a) with both species of the same initial size, and (b) with the species' initial sizes as they occur in nature. If *M. menidia* is indeed a superior exploitative competitor, it should win in both experiments (a) and (b).

Experiments could also be done using the fishes' natural food (e.g., copepods) rather than *Artemia*. Brine shrimp nauplii were chosen as the food in these experiments for standardization (it was assumed that species composition of collectible wild plankton would vary greatly during the course of the experiments). In addition, this *Artemia* strain's biochemical composition (Schauer *et al.*, 1980), pesticide burden (Olney *et al.*, 1980), and ability to support good growth and survival of Atlantic silversides (Beck *et al.*, 1980) were known. The caloric content of the *Artemia* used (5.603 kcal/g; Schauer *et al.*, 1980) was nearly identical to that of the copeod *Acartia tonsa* (5.664 kcal/g; Laurence, 1976), which silversides eat naturally.

An estimate of optimum food rations should ideally have been obtained before the competition experiments were conducted rather than after. If knowledge of feeding rates had been available at the start of the competition experiments, the fish densities or food rations used could have been altered to allow for better survival.

The applicability of laboratory experimentation to studies of competition for food by larval or juvenile fishes has been demonstrated here as well as by Laurence *et al.* (1981) and McComas & Drenner (1982). In particular, laboratory studies can answer questions that could never be addressed in the field. Increasing awareness of the importance of larval fish ecology (Braum, 1967, 1978; Cushing, 1974; Keast, 1980) indicates the need for more laboratory experimentation on competition between early life stages of fish.

Although McComas & Drenner (1982) also used *Menidia beryllina* as a competitor species, their experimental design and results were substantially different from those reported here. They found that *M. beryllina* can outcompete *Labidesthes sicculus* due to a difference in mouth morphology; *Menidia beryllina* has a protrusible, tube-shaped mouth, whereas *Labidesthes sicculus* has a forceps-shaped, open mouth. The two *Menidia* species used in the present study both have protrusible, tube-shaped mouths and exhibit considerable dietary overlap (Bengtson, 1984). The ability of *M. menidia* to outcompete *M. beryllina* appears to be due to a difference in the amount, rather than the kind, of food that is ingested, as demonstrated by the food ration experiments.

The results of the food ration experiments are enlightening when considered in the context of field biology of the two species. Apparently, *M. menidia* and *M. beryllina* have evolved different feeding strategies and requirements in relation to the different abundances of food available to young-of-the-year fish. *M. menidia*, spawning about a month earlier than *M. beryllina*, produce larvae and juveniles which feed on zooplankton during the yearly maximum of zooplankton production as measured in a Rhode Island estuary by Vargo (1974) and Bengtson (1984). They are thus adapted to an abundant food supply and respond to it with high consumption rates and rapid growth, the latter demonstrated by Barkman *et al.* (1981). They apparently also require more food (as a percentage of body weight) in order simply to stay alive. On the other hand, the later-spawning *M. beryllina* produce young which encounter much less food due to the sharp decline in zooplankton abundance which coincides with increased abundance of the ctenophore *Mnemiopsis leidyi* from mid-summer through autumn (Vargo, 1974;

Hulsizer, 1976). Their apparent adaptation to a scarce food supply is a lower consumption rate and slower growth (Bengtson, 1984) than that of *Menidia menidia*. The respiration rate of *M. menidia* is also generally higher than that of *M. beryllina* (Ashton, 1973).

Estimates of the feeding rates of the two *Menidia* species obtained during this study have been used to determine whether food is a limiting resource in nature (Bengtson, 1984). Results of the experiments indicate not only the amount that each species is capable of eating for maximum survival and growth, but also the minimum amount necessary for survival and maintenance of body weight. Quantitative sampling data on field fish and zooplankton, conducted in conjunction with these laboratory experiments but reported elsewhere (Bengtson, 1984), indicated that food is limiting in the estuary in the sense that maximum survival and growth of all postlarvae is not attained.

Although dry weights of fish were not measured during this experiment, *Menidia* of both species in the size ranges tested are $\approx 75\%$ water and the wet *Artemia* rations are $\approx 90\%$ water (Bengtson, unpubl. data). *Menidia menidia*, therefore, is capable of consuming ≈ 50–100% of body weight per day on a dry weight fish–dry weight food basis. I have found no indication in the literature that any other fish tested has shown such a high rate of consumption and the figure is much higher than those maximum rations for salmonid species listed by Brett (1979). In the future, it would be instructive to study the energetics of this profligate consumer to determine its effect on the estuarine system.

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